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Ultrastructure of the Male Gonad and Spermatogenesis in the Lesion Nematode, *Pratylenchus penetrans* (Nemata: Pratylenchidae)

BURTON Y. ENDO,[1] ULRICH ZUNKE,[2] AND WILLIAM P. WERGIN[1]

[1] U.S. Department of Agriculture, Agricultural Research Service, Plant Sciences Institute, Nematology Laboratory, Beltsville, Maryland 20705-2350 and

[2] Universtät Hamburg, Institut für Angewandte Botanik, Marseiller Strasse 7, 20355 Hamburg, Germany

ABSTRACT: Transmission electron microscopy was used to elucidate the structural anatomy of the male reproductive system of *Pratylenchus penetrans*. The male gonad has an elongated telogonic testis with a single row of spermatogonia in the germinal zone. The spermatogonia increase in size to spermatocytes in the growth zone. The spermatocytes then undergo meiosis to form spermatids. Synaptonemal complexes in the spermatocytes signify the pachytene stage of the first meiotic division. Spermatids are characterized by an abundance of fibrous bodies surrounding prominent electron-opaque spheroid nuclei. Spermatids in the proximal region of the seminal vesicle are transformed to spermatozoa as they accumulate in the seminal vesicle. During this process, filopodia decrease in number, residual bodies are lost, and sperm nuclei become irregularly shaped and surrounded by mitochondria and fibrous bodies. Spheroid spermatozoa retain a modified morphology with large sectors of flocculent cytoplasm devoid of cellular organelles. The electron-transparent region of the sperm extends into a pseudopod that controls the crawling form of motility that is typical of the spermatozoa of many nematode species. Seminal fluid produced by cells of the vas deferens accumulates and appears to cause aggregation of sperm within the seminal vesicle. Sperm morphology in the spermatheca of female specimens is similar to that in the vas deferens of the male.

KEY WORDS: electron microscopy, lesion nematode, male gonad, *Pratylenchus penetrans*, spermatogenesis, testis, ultrastructure.

The feeding habits and pathogenicity of *Pratylenchus penetrans* and related species of the lesion nematode have been well documented (Dropkin, 1989; Townshend and Stobbs, 1981; Townshend et al., 1989; Zunke and Institut für den Wissenschaftlichen Film, 1988; Zunke, 1990a, b). Previous light-microscopic studies have provided a basis for understanding gametogenesis, embryogenesis, and postembryogenesis in several species of *Pratylenchus*, including *P. penetrans* (Roman and Hirschmann, 1969; Roman and Triantaphyllou, 1969). Electron microscopic studies have depicted the structure of the male copulatory organs of *P. penetrans* (Wen and Chen, 1976; Mai et al., 1977; Bird and Bird, 1991) and spermatogenesis and sperm morphology in the cyst nematodes *Globodera rostochiensis* (Wollenweber, 1923) Behrens, 1975, *G. virginiae* (Miller and Gray, 1968) Behrens, 1975, *Heterodera schachtii* Schmidt, 1871, and *H. avenae* Wollenweber, 1924 (Shepherd et al., 1973). To identify new phylogenetic characters in the Heteroderinae, the fine structure of *Verutus volvingentis* was compared with that of *Meloidodera floridensis*. The study compared sperm size, distribution of filopodia, condition of chromatin after insemination, and persistence of fibrous bodies (Cares and Baldwin, 1994a). In *Ekphymatodera thomasoni*, the sperm originated from germ cells connected to a central rachis (Cares and Baldwin, 1994b). This character was shared with *Globodera* but not with other Heteroderinae. Fibrous bodies were abundant in spermatids but did not persist in sperm of *Ekphymatodera* as they did in sperm of *Meloidodera* and *Verutus* (Cares and Baldwin, 1994a, b).

In a recent review, Scott (1996) emphasized that nematode sperm did not contain actin or myosin. This observation could account for the crawling motility of spermatozoa. The review summarized that locomotion of nematode sperm appeared to depend on a simple cytoskeleton consisting of small, basic sperm-specific proteins that were designated as major sperm proteins (MSP). The MSP were synthesized in spermatocytes and assembled in cytoplasmic paracrystalline arrays or fibrous bodies. After meiosis, fibrous bodies segregated into the cytoplasm of developing spermatids. After spermatid budding or separation from the residual body, the fibrous bodies disassembled and the MSP were released into the cytoplasm where they were maintained in an unpolymerized state.

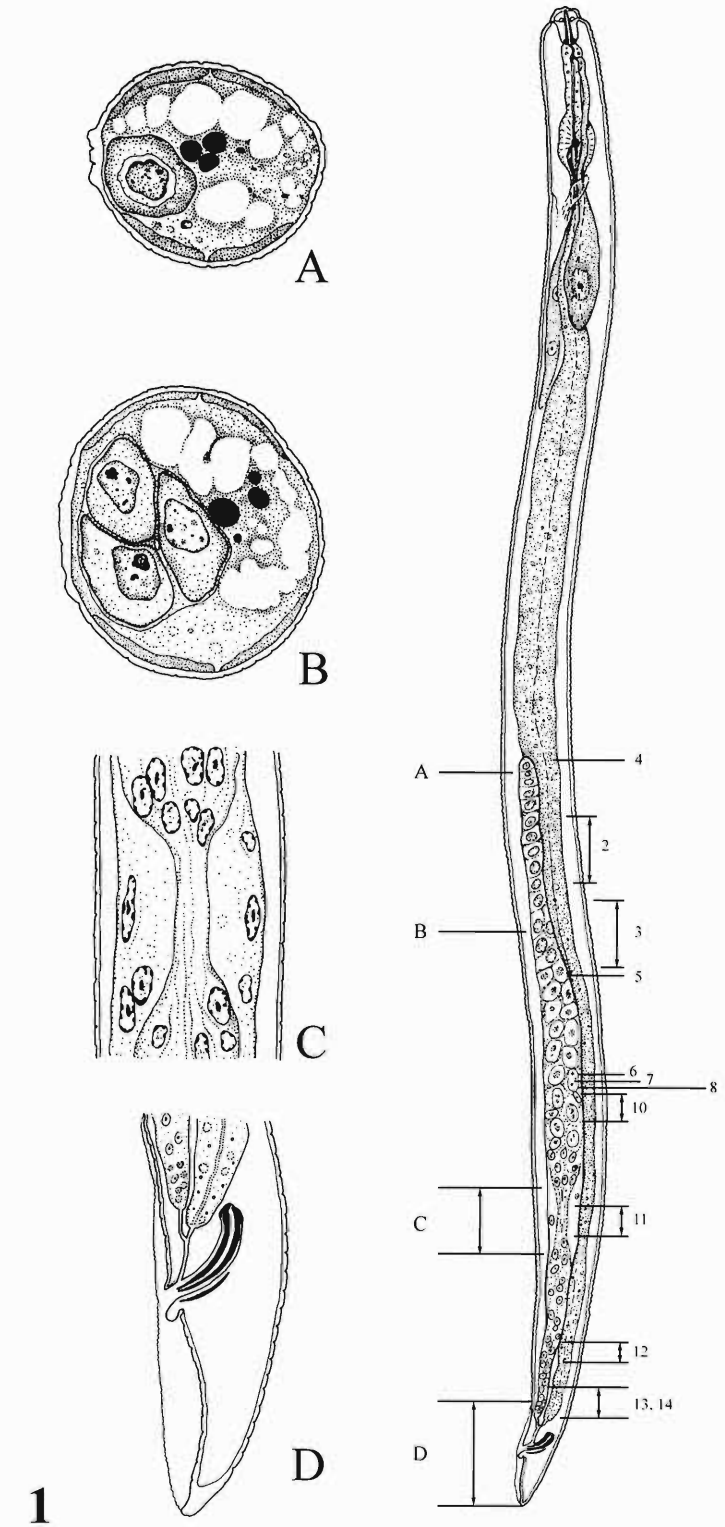

Figure 1. Male specimen of *Pratylenchus penetrans* emphasizing gonad morphology. Numbers indicate approximate sites of the gonad. A = spermatogonium; B = spermatocytes; C = spermatozoa; D = spicules.

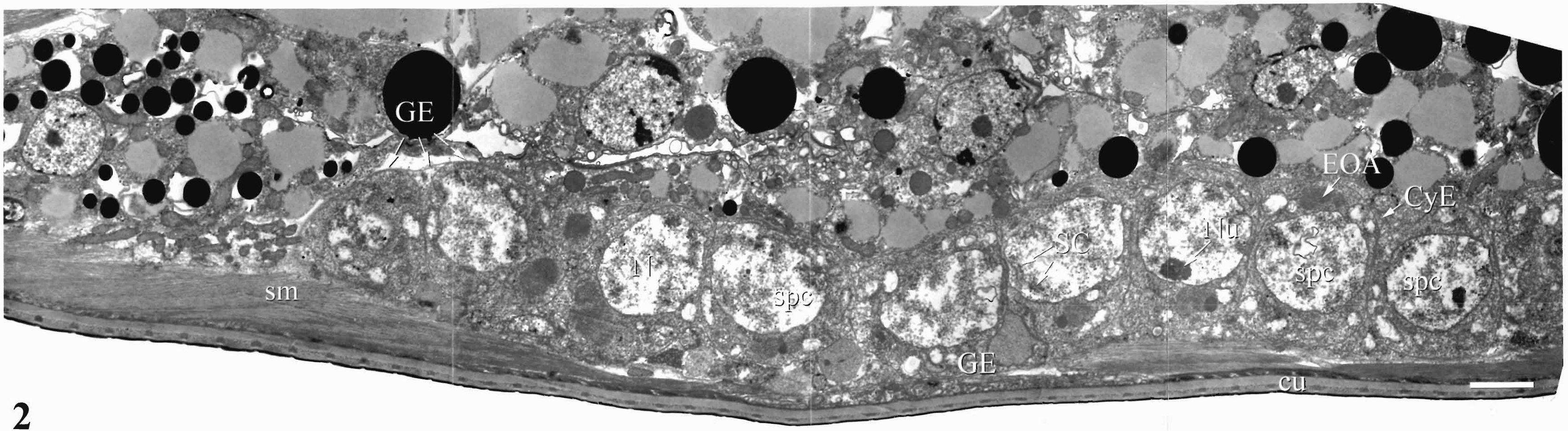

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Figure 2. Distal region of male gonad of *P. penetrans* showing single row of cells enclosed by gonad epithelium (GE). Most cells show prominent nuclei (N) with enclosed fragments of synaptonemal complexes (SC) that join 2 paired homologous chromosomes at pachytene stage of meiosis. Membrane invaginations (CyE) of gonad epithelium partially fill the spaces between the spermatocytes. cu = cuticle; EOA = electron-opaque accumulation; Nu = nucleolus; sm = somatic muscle. Scale bar = 1.0 μm.

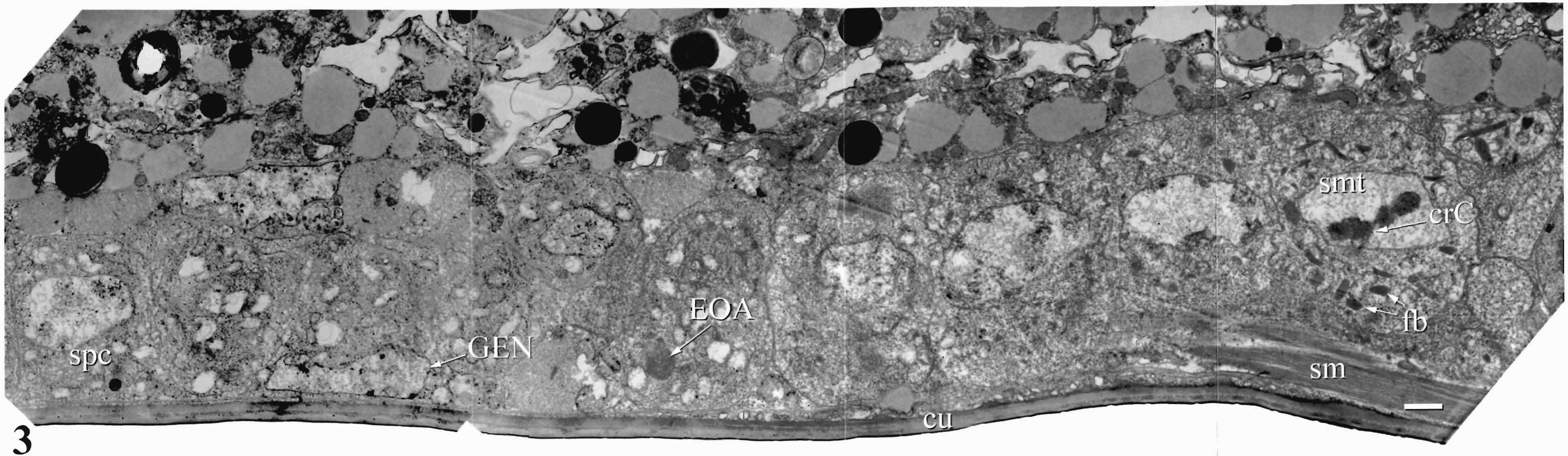

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Figure 3. Longitudinal section of the same specimen shown in Figure 2, illustrating the transitional zone of the testis of *P. penetrans*. Spermatocytes (spc) undergo meiosis to form spermatids (smt). Early stage of spermatid development indicated by chromatin clumping (crc) and appearance of fibrillar bodies (fb). cu = cuticle; EOA = electron-opaque accumulations; GEN = gonad epithelial nucleus; Sm = somatic muscle. Scale bar = 1.0 μm.

The MSP became concentrated in the pseudopods where they were reassembled into filaments. The composition and role of the fibrous bodies that occur in spermatids and sperm of *P. penetrans* and related plant-parasitic species have not been determined.

In a recent study, we used transmission and low-temperature scanning electron microscopy to observe the anatomy of the esophagus, intestine, and reproductive system of *P. penetrans* (Cobb, 1917) Sher and Allen, 1953 (Endo et al., 1997). The current study continues observations on the ultrastructure of the male reproductive system of *P. penetrans*. We examined morphological features of the male gonad along with the development of spermatocytes into spermatids, the storage of spermatids and sperm within the seminal vesicle, and sperm assembly and passage through the vas deferens.

Materials and Methods

Specimens of *P. penetrans* were obtained from root cultures of corn (*Zea mays* L. 'Iochief') grown in Gamborg's B-5 medium without cytokinins or auxins (Gamborg et al., 1976). Adults and juveniles were collected from infected root pieces that were incubated in water. The samples were prepared for electron microscopy as previously described (Endo and Wergin, 1973; Wergin and Endo, 1976). Nematodes, which were embedded in 2% water agar, or infected root segments were fixed in buffered 3% glutaraldehyde (0.05 M phosphate buffer, pH 6.8) at 22°C for 1.5 hr, washed for 1 hr in 6 changes of buffer, postfixed in buffered 2% osmium tetroxide for 2 hr, dehydrated in an acetone series, and infiltrated with a low viscosity embedding medium (Spurr, 1969). Silver-gray sections were cut on an ultramicrotome with a diamond knife and mounted on uncoated 75- × 300-mesh copper grids. The sections were stained with uranyl acetate and lead citrate and viewed in a Philips 301 or 400T electron microscope operating at 60 kV with a 30-μm objective aperture.

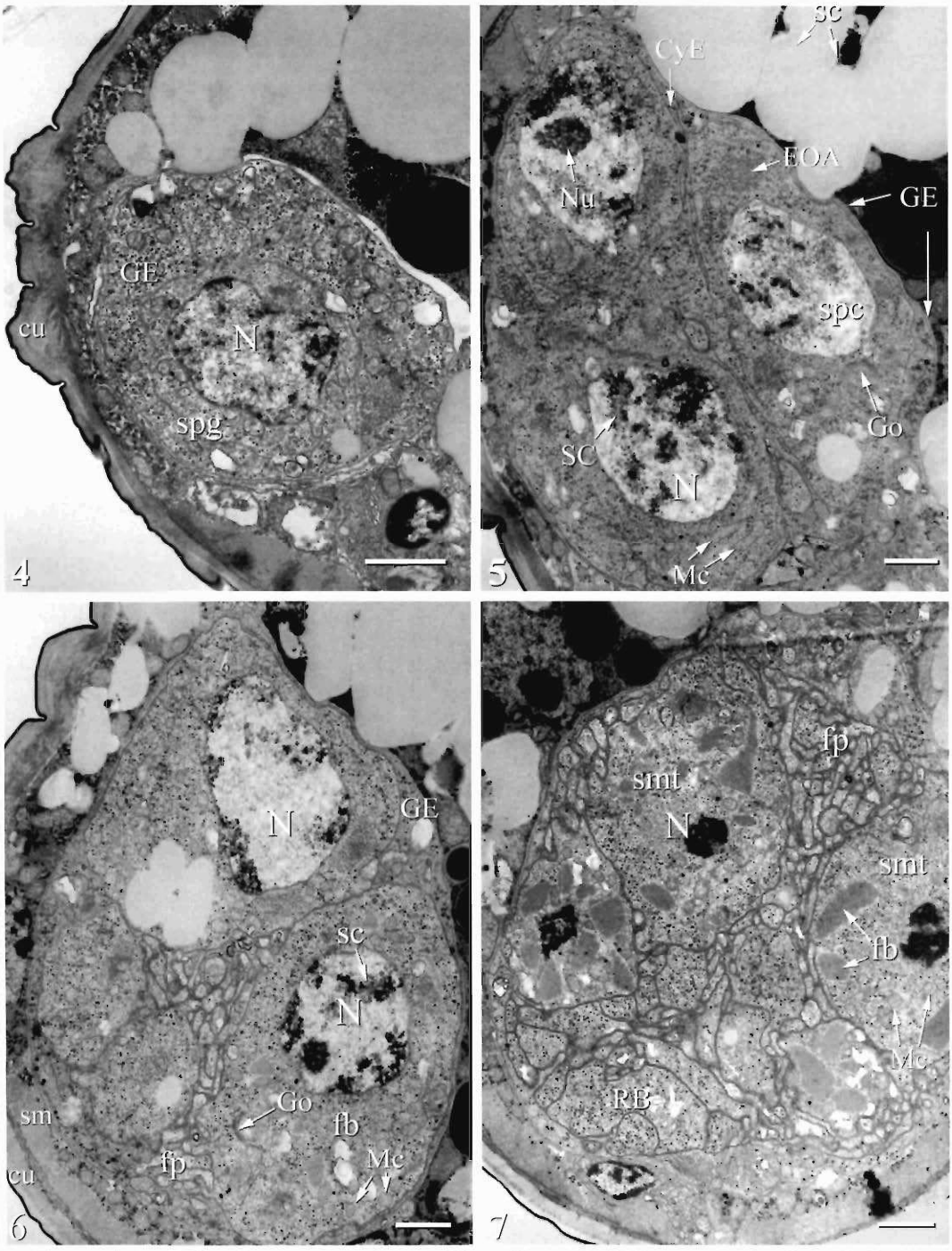
Results

The male gonad of *P. penetrans* has a mean length of 234 μm and a width of 14.5 μm within a body length of 520 μm and body width of 20 μm (Fig. 1). The most distal region of the testis contains a single row of cells comprising spermatogonia of the germinal zone of the testis (Figs. 4–7). Linearly arranged spermatocytes of the testis contain synaptonemal complexes that occur during pachytene stage of meiosis (Fig. 2). An abrupt increase in girth of the testis occurs in the region where spermatocytes accumulate as multiple rows of cells that undergo meiosis and cellular division to produce spermatids (Fig. 3). The spermatozoa, developing from spermatids, fill the seminal vesicle that extends through a major sector of the gonad and joins the multicellular, glandular vas deferens (Fig. 1).

The telogonic testis of *P. penetrans,* is characterized by several portions of synaptonemal complexes within the spermatocytes. These complexes, which occur at the pachytene stage of prophase during the first meiotic division (Figs. 2, 5, 8, 9), have 2 lateral elements, each with chromatin of sister chromatids and a central striated element (Figs. 2, 5, 8, 9). Additional chromatin is dispersed throughout the nucleoplasm, which is delineated by the nuclear membrane. Depending on the stage of division, the nuclei also contain distinct nucleoli (Figs. 2, 5). The cytoplasm of spermatocytes contains rough endoplasmic reticulum, free ribosomes, mitochondria, Golgi bodies, and clusters of electron-opaque masses that can appear granular, fibrillar, or paracrystalline (Figs. 2, 5, 6). The closely appressed spermatocytes are retained within the gonad epithelium, which extends between the cells of the gonad (Figs. 2, 5, 6). The spermatocytes are associated with a modified central rachis consisting of a cylindroid cytoplasmic unit located at the center of rows of spermatocytes (Figs. 5, 6).

Beyond the linearly arranged row of spermatocytes, which are located along the lateral chord, the gonad epithelium widens as each of the spermatocytes undergoes 2 divisions to form 4 spermatids (Figs. 1, 7). During this process, chromatin tends to accumulate inside the nuclear membrane; shortly thereafter, the membrane breaks down (Fig. 6). The chromatin of the spermatid aggregates in a electron-opaque spherical unit, which is surrounded by clusters of fibrous elements, Golgi bodies, and mitochondria (Figs. 7, 10). In individual spermatids, the cytoplasm, which becomes flocculent and electron translucent, contains a highly condensed nucleus, mitochondria, and fibrous bodies (Figs. 7, 10, 11). Portions of the limiting membrane of the spermatids evaginate to form filopodia that have cytoplasmic, microtubular, and filamentous continuity with the central body. Microtubules also accumulate along the inner surface of the membrane of spermatids and spermatozoa (Figs. 10, 11).

The structural transition from spermatids to spermatozoa is not morphologically distinct. The



Figures 4–7. Series of transverse sections of the male gonad of *P. penetrans* showing a single row of cells in the most distal region of the gonad and its relation to multiple cells in the transitional zone that leads to spermatid formation and aggregation. 4. Single spermatogonial (spg) cell within the boundaries of the gonad epithelium (GE). cu = cuticle; N = nucleus. 5. Testis in the expanding region of the gonad showing 3 tightly arranged spermatocytes (spc) surrounded by gonad epithelium (GE) that extends into the interspermatocyte spaces (CyE). Spermatocytes with prominent nuclei (N) have cytoplasm with free

spermatozoa tend to be spherical to oblong with considerable variation in shape and organelle content, depending on the site of the section (Fig. 12). Membrane evaginations form filopodia similar to those found in newly formed spermatids (Figs. 10, 11). Sperm near the terminus of the vas deferens occasionally lack filopodia (Fig. 13. The nuclei of sperm are electron opaque, similar to those observed in spermatids. Mitochondria and narrow strands of fibrous bodies occur near the chromatin masses of each sperm nucleus, whereas a large region of the spheroid or elongated cell is often devoid of organelles and merely contains flocculent cytoplasm. This region, when elongated, probably functions as a pseudopod (Figs. 12, 14) that is used for movement of sperm in the uterus. Spermatids and sperm are contained within an elongated membrane-bound region termed the seminal vesicle (Figs. 1, 12). The seminal vesicle usually is filled with sperm and spermatids, but large sectors may be filled with electron-transparent material, possibly seminal fluid, that arises from secretions by the glandular cells of the vas deferens (Figs. 13, 14). The electron-transparent fluidlike region of the vas deferens may be interrupted by elongated strands and clumps of material resembling collapsed filopodia and remnants of residual bodies of spermatids (Fig. 11). The distal region of the vas deferens (Fig. 13) contains electron-transparent to -opaque secretory granules that apparently are derived from secretory cells at the base of the vas deferens (Fig. 14). The cells of this proximal region of the vas deferens (Fig. 14) contain numerous electron-opaque secretory granules and associated Golgi bodies. The juncture of the lumen of the vas deferens and the rectal canal was obscure in thin sections but their terminal openings join posteriad to form the cloaca.

Spermatozoa, which are located in the proximal region of the seminal vesicle and adjacent to the cellular region of the vas deferens (Fig. 13), are similar in morphology to sperm observed in the spermatheca of the female gonad (Fig. 15). In general, the spermatozoa lack filopodia, which are abundant on the spermatid and on the sperm located at the distal end of the seminal vesicle. The spermatozoa of the male and those present in the spermatheca of the female are also similar in their distribution of cellular organelles. In the spermatheca, the nuclei, mitochondria, and a few fibrous strands of fiber bodies occur at 1 end of the sperm, and the other end, which is almost devoid of organelles, is filled with flocculent cytoplasm. The chromatin of the nuclei is concentrated but irregular in shape (Fig. 15). The nuclei tend to be crescent shaped and differ from the spheroid, highly electron-dense nuclei of spermatids (Figs. 10, 11). Membrane specialization or membrane organelles do not appear to form along the inner boundary of sperm or spermatids of this species.

Discussion

Fragments of synaptonemal complexes within pachytene nuclei in spermatocytes of *P. penetrans* structurally resemble synaptonemal complexes described in spermatocytes and oocytes of *Ascaris suum* (Goldstein and Moens, 1976), and in oocytes of various plant-parasitic species, including *Meloidogyne hapla* (Goldstein and Triantaphyllou, 1978), *M. spartinae* (Goldstein and Triantaphyllou, 1995), *Heterodera glycines* (Goldstein and Triantaphyllou, 1979), and many other organisms (for review, see Westergaard and von Wettstein, 1972). The ultrastructure of the synaptonemal complexes, which occur as incomplete units in *P. penetrans,* resembled that of the reconstructed synaptonemal complexes

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ribosomes, rough endoplasmic reticulum, mitochondria (Mc), Golgi bodies (Go), and moderate electron-opaque accumulations (EOA). Nuclei of the primary spermatocytes in the cross-section of testis show synaptonemal complexes (SC) indicative of the pachytene stage of the first meiotic division. 6. Testis shows 2 spermatocytes containing nuclei with intact membranes. One of the spermatocytes has synaptonemal complexes (SC) in the nucleus (N) and fibrillar bodies (fb) within the cytoplasm. The other nucleated cell showing dispersed chromatin is probably a primary spermatocyte at diplotene. Filopodia (fp) between the cells indicate that the section is near the developing spermatids or sperm in the male gonad. cu = cuticle; GE = gonad epithelium; Go = Golgi apparatus; Mc = mitochondrion; Sm = somatic muscle. 7. Broad region of the testis shows an accumulation of several spermatids (smt) in the midst of filopodia (fp) and other cell components that include residual bodies (RB). Early stages of spermatid formation characterized by dense clumping of nuclear (N) chromatin and absence of discernable nuclear membranes. The major organelles in the cytoplasm are fibrous bodies (fb) and mitochondria (Mc). Scale bars = 1.0 μm.

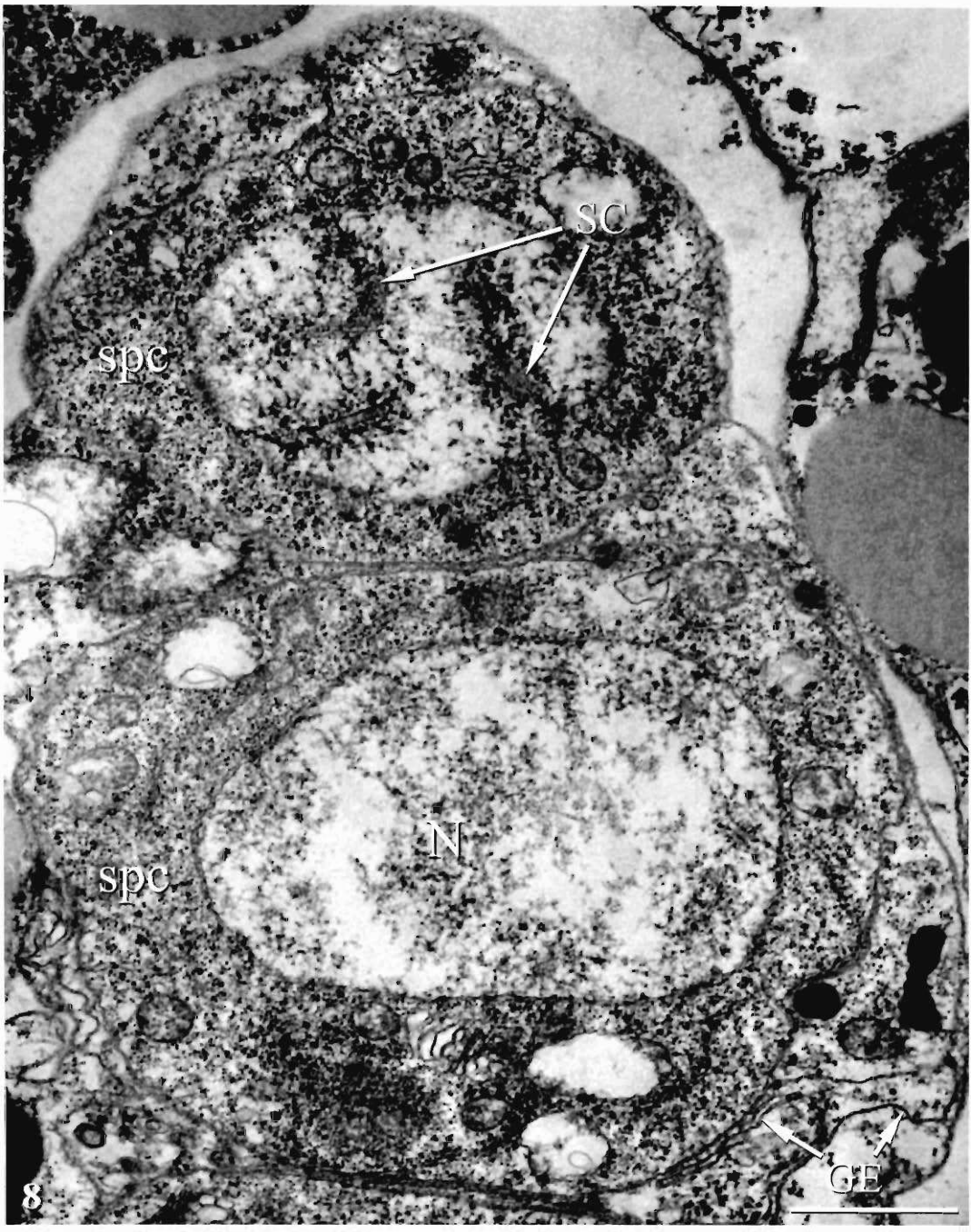


Figure 8. Longitudinal section of 2 spermatocytes (spc) near site of spermatid development in gonad of *P. penetrans*. Tangential section of a nucleus (N) of 1 spermatocyte shows parts of synaptonemal complexes (SC). GE = gonad epithelium. Scale bar = 1.0 μm.

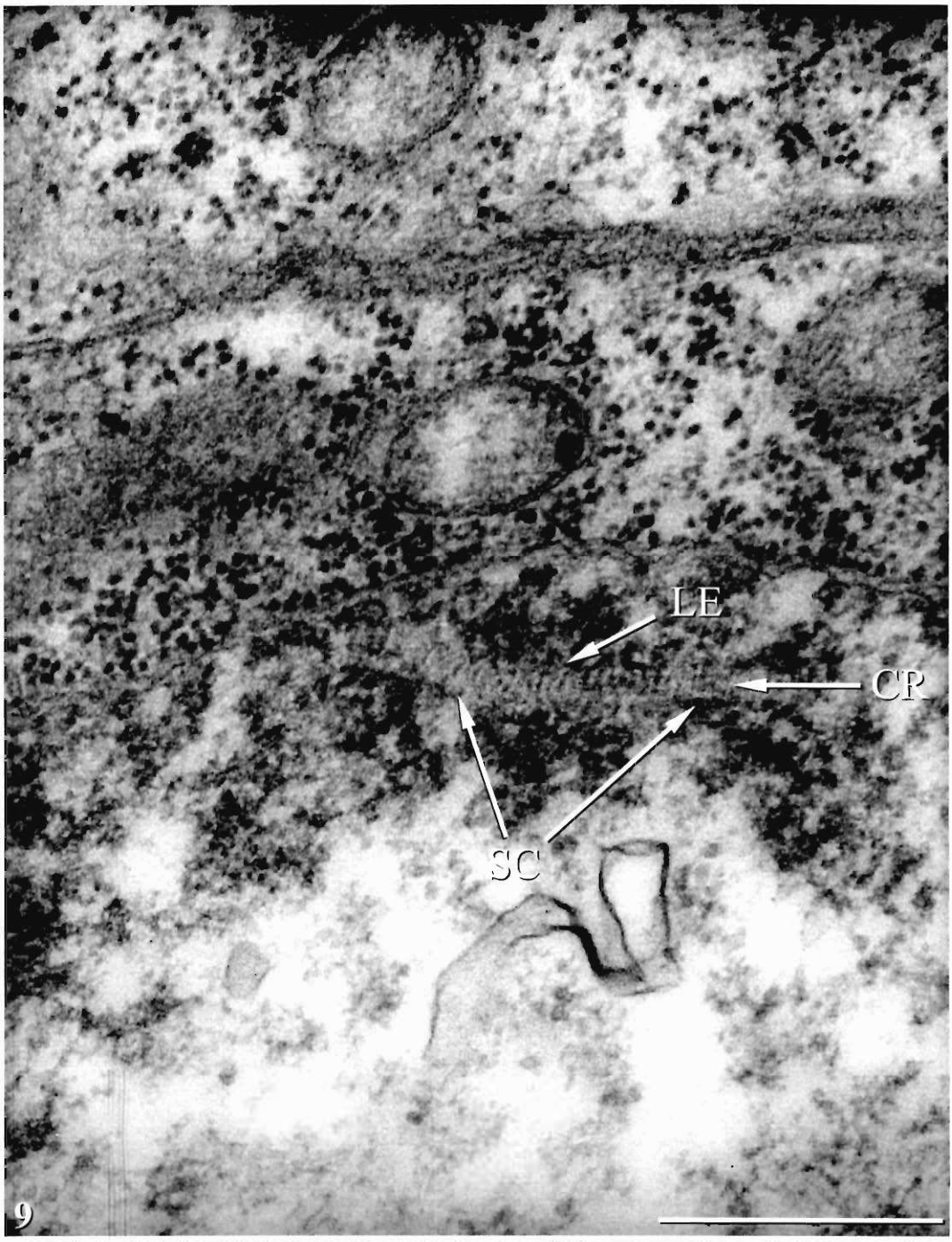
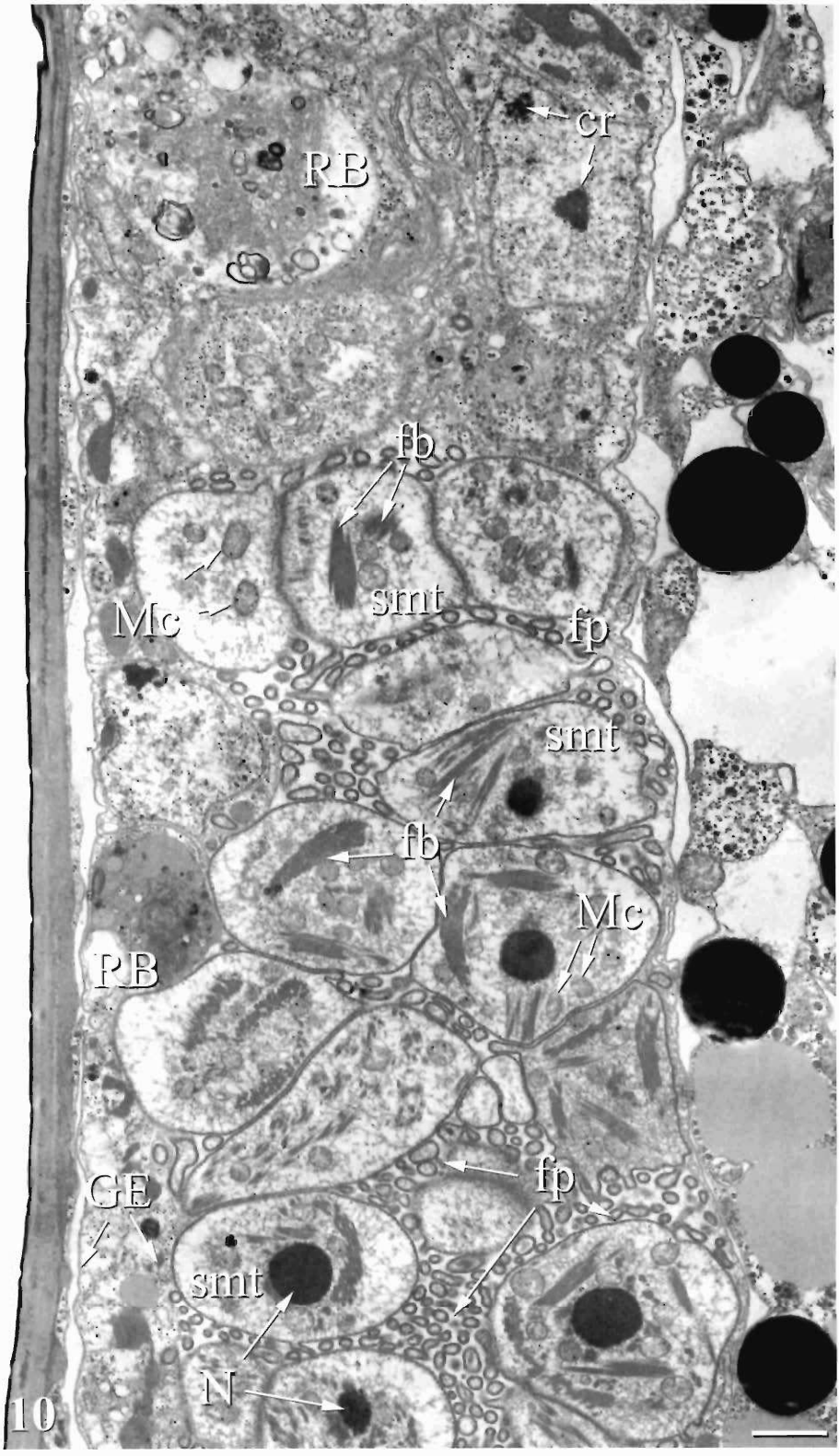


Figure 9. Enlargement of synaptonemal complex (SC) during pachytene in spermatocyte of *P. penetrans*. CR = central region; LE = lateral element. Scale bar = 0.5 μm.



observed in oocytes and spermatocytes of *Ascaris lumbricoides suum* (Goldstein and Moens, 1976). In both nematodes, the complexes had lateral amorphous elements and a central striated element. In contrast, at meiotic pachytene, the synaptonemal complexes in oocytes of several species of *Meloidogyne,* with the exception of *M. microtyla,* were bipartite and consisted of 2 lateral elements; a central striated element was lacking. *Meloidogyne spartinae* had 7 synaptonemal complexes signifying a 1N haploid chromosome count for this species (Goldstein and Triantaphyllou, 1995). The number of synaptonemal complexes of *P. penetrans* has not been determined; however, the structure of the synaptonemal complexes of spermatocytes is similar to that in oocytes of *Meloidogyne,* with their central striated elements bordered by lateral elements.

The testes of most male gonads of nematodes are similar (Foor, 1983). The testis is a single tubular organ composed of a blind terminal end where germ cells form and an elongate region where spermatocytes enlarge and differentiate into spermatids and spermatozoa. Nematode sperm differ from those of most other organisms in that they may be rounded, conical, lobate, or elongate. Furthermore, they lack flagella and acrosomes. Moreover, in some nematodes, the spermatozoa in the seminal vesicle of a male may be round and nonmotile but can become amoeboid and motile when transferred into a female gonad (Foor, 1970). Many investigators assume that spermatozoan changes occur in response to substances present in the female reproductive system. However, studies of *A. lumbricoides* have provided evidence that spermatozoan changes actually originate in the glandular vas deferens of the male gonad (Foor and McMahon, 1973; Foor, 1976). For example, when materials from the vas deferens of *A. lumbricoides* were injected into the seminal vesicle of an *Ascaris* male, the normally enclosed spherical cells, which contained mitochondria, dense lipidlike particles, a non-membrane-bound nucleus, and numerous membranous elements or organelles, became transformed. Lipidlike particles coalesced to form large refringent bodies, membrane specializations fused with the plasma membranes, and prominent pseudopods were formed (Foor, 1970).

The influence of seminal fluid on spermatozoan morphology has not been determined in *P. penetrans.* Although the plasma membranes of

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Figure 10. Longitudinal section through transitional zone of the testis of *P. penetrans* showing spermatid formation and maturation. Lateral anterior view of the testis shows cells without nuclear membranes prior to the aggregation of chromatin (cr) into electron-dense spheroid nuclei. Enlarged cells adjacent to developing spermatids appear to be residual bodies (RB), which are nonnucleated regions that are sloughed during spermatid maturation. The proximal region of the transitional zone shows spermatids (smt) with characteristic fibrous bodies (fb) and mitochondria (Mc). Filopodia (fp) are formed from outer membrane evaginations. Sections through some spermatids show electron-opaque spheroid nuclei (N) without discernable nuclear membranes. Cellular bodies along the gonad epithelium (GE) appear to be residual bodies. Scale bar = 1.0 μm.

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Figure 11. Longitudinal section though the proximal sector of the vas deferens of *P. penetrans* showing a centralized accumulation of spermatids (smt) surrounded by broad region of electron-transparent seminal fluid (sf) containing remains of Golgi bodies (RGo) and filopodia (Rfp). Spermatid body shape ranges from ovoid to oblong. cu = cuticle; fp = filopodia. Scale bar = 1.0 μm.

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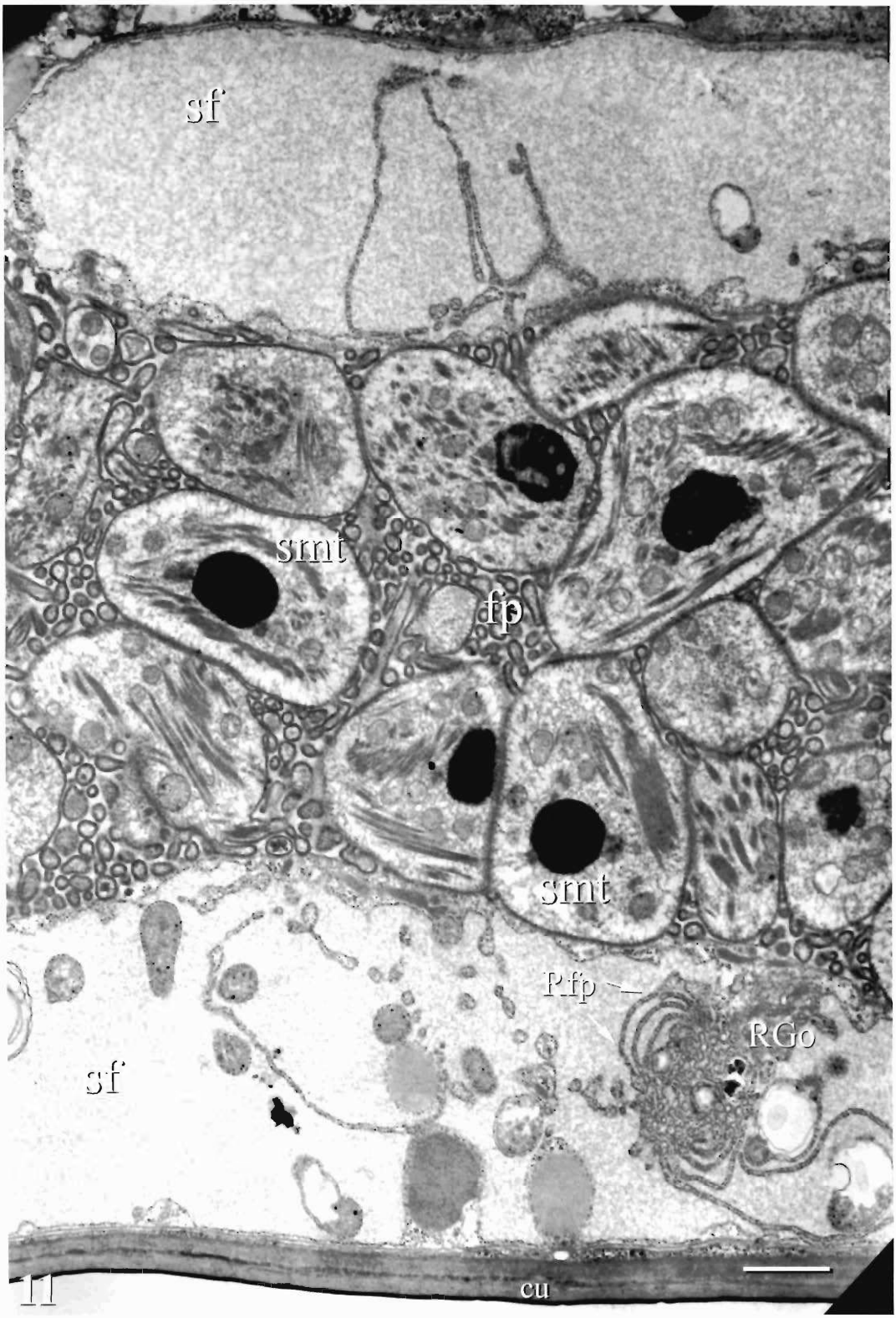
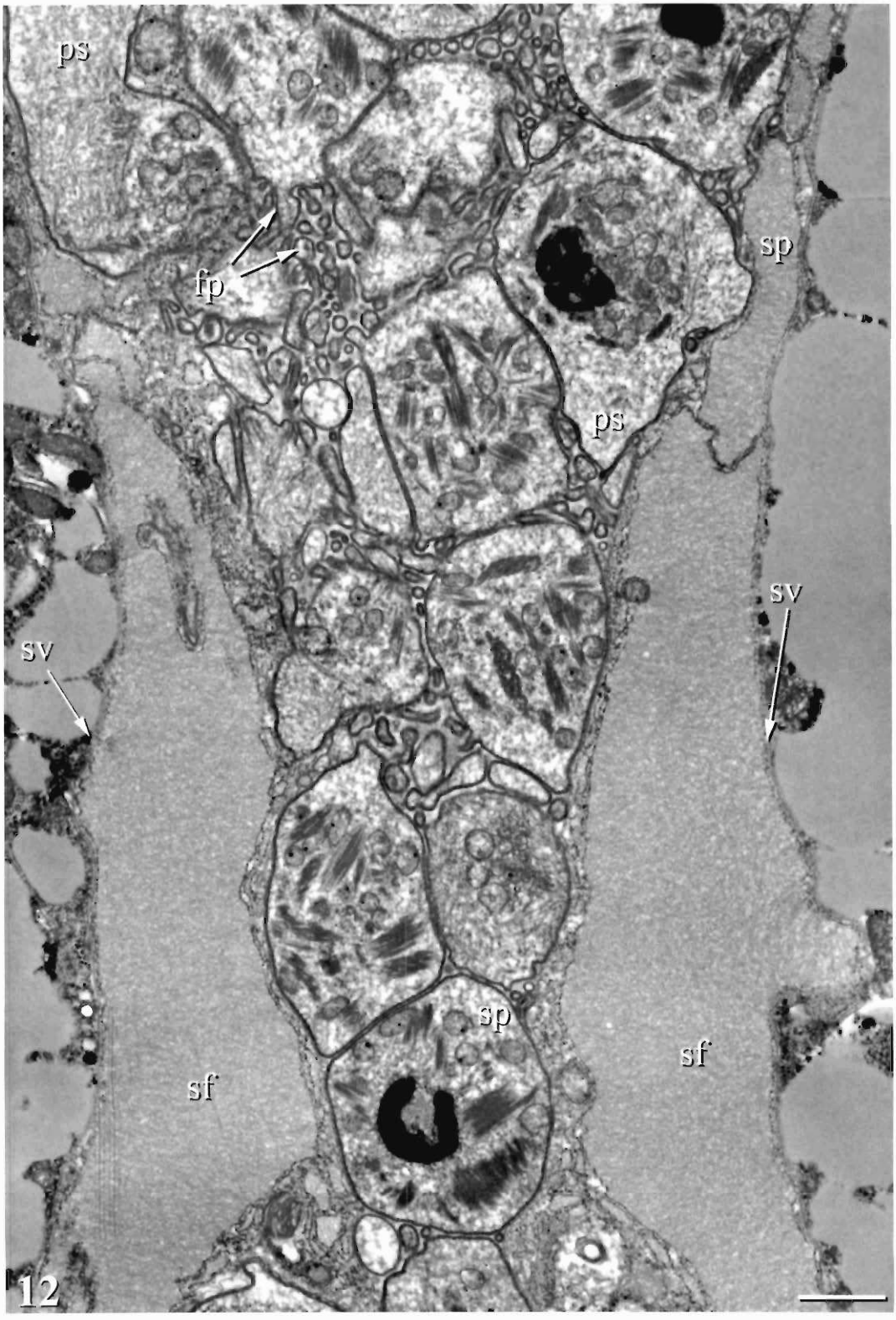
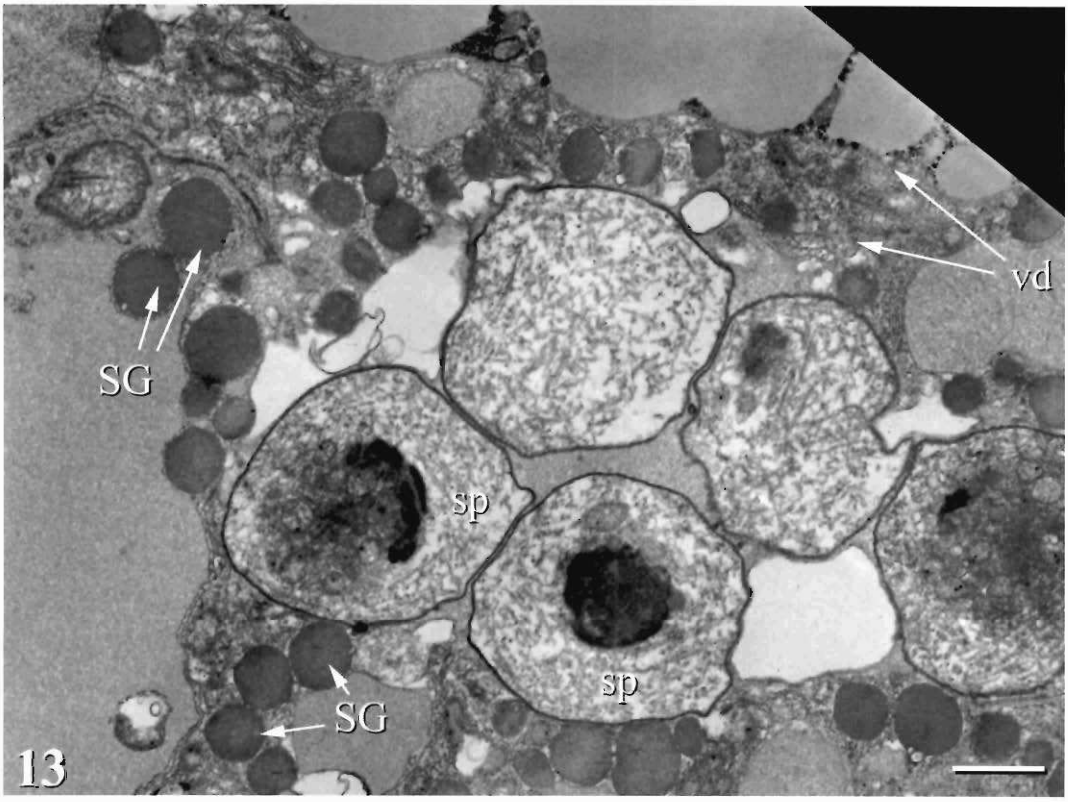
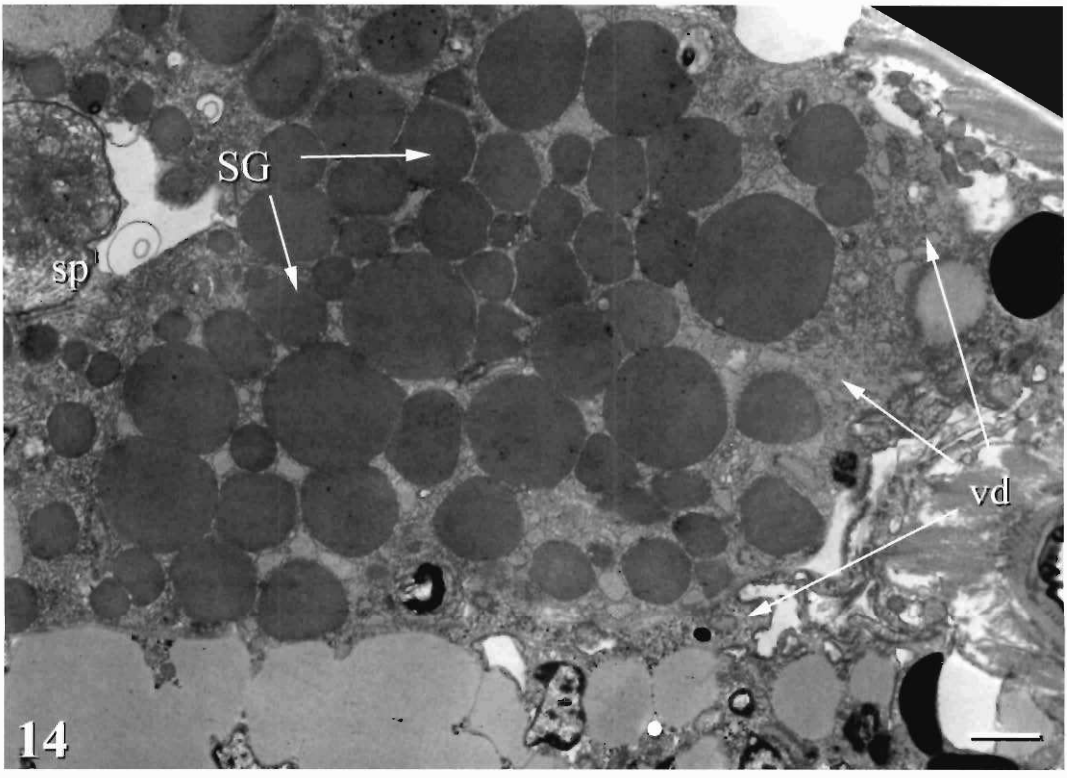
Figure 12. Longitudinal section of the vas deferens of *P. penetrans* showing a region filled with seminal fluid (sf) in which sperm (sp) are localized prior to ejaculation. Filopodia (fp) of mature spermatids and sperm are greatly reduced in number. Mitochondrial and fibrous bodies accumulate around irregularly shaped nuclear chromatin, and a flocculent cytoplasm, usually devoid of organelles, characterizes the pseudopodial (ps) extensions. Spermatozoa appear to be at a more advanced stage of spermatozoan development than those shown in Figure 11. sv = seminal vesicle. Scale bar = 1.0 μm.









spermatozoa at the most distal portion of the seminal vesicle usually are associated with numerous filopodia, these structures rarely occur on spermatozoa located at the base of the vas deferens or in the spermatheca of inseminated females. The fragments of filopodia and other cellular remnants, consisting of organelles such as Golgi bodies within large masses of electron-translucent material, may be part of a transformation in which filopodia are separated from the plasma membrane of the maturing spermatozoan. In *G. rostochiensis* males, similar fragments of filopodia were reported in the fluid within the seminal vesicle of the vas deferens (Shepherd et al., 1973).

The sperm of *P. penetrans* do not contain the prominent lipidlike mass called a refringent body, which is unique among ascarids. Furthermore, sperm of *P. penetrans* do not have the membrane specializations that occur in many of the animal-parasitic and microbivorous species, such as *Caenorhabditis elegans* (Wolf et al., 1978). Membrane specializations in the insect-parasitic species *Heterorhabditis bacteriophora* are closely associated with the fibrous bodies of sperm (Poinar and Hess, 1985). Among the plant-parasitic species, membrane specializations occur in the sperm of the vermiform *Aphelenchoides blastophthorus* (Shepherd and Clark, 1976) but are lacking in sperm of cyst nematodes, *Heterodera* and *Globodera* spp. (Shepherd et al., 1973). Membranous organelles are prominent in spermatocytes but disappear in the older spermatids of *Xiphinema theresiae* (Kruger, 1991). Membrane specializations, also called membrane organelles, arise in the spermatocytes and may combine with the fibrous body to form a membrane complex that appears to be important in the delivery and storage of sperm protein. In the mature sperm, a glycoprotein released by the membrane organelle may be important for sperm motility (Kimble and Ward, 1988; Scott, 1996). In the absence of these membrane organelles in *P. penetrans,* the mechanism for sperm protein assembly and sperm release may differ.

Spermatozoa of *P. penetrans* have prominent pseudopods similar to those described in animal-parasitic species (Foor, 1970), plant-parasitic species including *G. rostochiensis* (Shepherd et al., 1973) and *E. thomasoni* (Cares and Baldwin, 1994b), and free-living forms such as *C. elegans* (Wolf et al., 1978). Pseudopod morphology and activity, as they relate to sperm motility, have been discussed in a recent review (Scott, 1996). Sperm motility, along with other features unique to nematodes, were highlighted as potential targets for control of human-parasitic species. Those targets included 1) disrupting early events of spermatogenesis to inhibit sperm maturation, 2) blocking processes that activate spermatid maturation, and 3) obstructing molecules involved in maintaining sperm positions in the spermatheca or blocking molecules involved in sperm–egg recognition (Scott, 1996). Whether nematode reproduction can be inhibited will depend on the unique components that contribute to spermatogenesis and their possible disruption.

In *P. penetrans,* the abundance of fibrous elements in the cytoplasm of spermatids, and to a lesser extent in spermatozoa, is very similar to that described in *Heterodera* and *Globodera* spp. The fibrous elements appear to form spontaneously. Although the initially large masses present in spermatids are gradually replaced, they are retained in sperm of *H. schachtii* but are dispersed in *G. rostochiensis* (Shepherd et al., 1973). Similarly, fibrous elements of *P. penetrans* occur in large masses in spermatids and are retained as narrow elongated strands in spermatozoa. These strands accumulate in the seminal vesicle and vas deferens of the male gonad and within the spermathecae of inseminated females. Fertilization of oocytes occurs in a specialized region of the uterus, the spermatheca, and in the uterine duct (Bird and Bird, 1991). Scott (1996) discussed the role of paracrystalline

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Figures 13, 14. Longitudinal section of the basal region of the vas deferens of the *P. penetrans* specimen of Figure 12. 13. A group of spermatozoa (sp) within the vas deferens (vd) channel supported by tissue containing secretory granules (SG) in various stages of dispersal. 14. Extension of Figure 13 illustrating the basal terminus of the vas deferens (vd), where electron-opaque secretory granules (SG) dominate the contents of supporting cells of the vas deferens. sp = sperm. Scale bars = 1.0 μm.

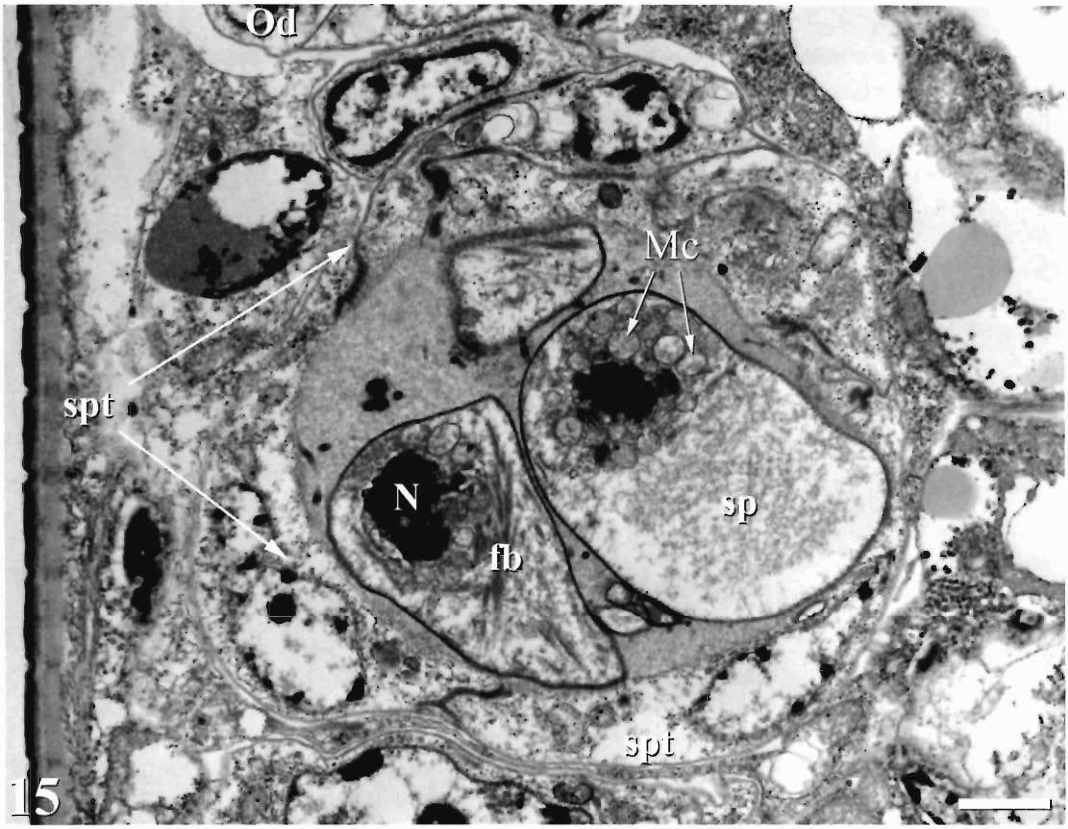

Figure 15. Longitudinal section through a female specimen of *P. penetrans* showing spermatozoa (sp) within the spermatheca (spt). Two of the spermatozoa show the mitochondria (Mc) closely surrounding the nuclear (N) chromatin. Od = oviduct. Scale bar = 1.0 μm.

arrays or fiber bodies synthesized in spermatocytes and their role in nematode sperm motility. Instead of the crawling motility of nematode sperm being dependent on actin or myosin, locomotion apparently depends on a simple cytoskeleton derived primarily from a family of small, basic MSP (Scott, 1996). MSP genes in various copy numbers have been identified in over 25 nematode species representing 20 genera (Scott, unpubl.). In observing the development and motility of sperm in *C. elegans,* Nelson et al. (1982) used gel electrophoresis to show that actin, a common component of motile systems, comprised only 0.02% of the total protein in sperm. Apparently, 1 of the MSP is the major component of *C. elegans* and *Ascaris* sperm. This small polypeptide, which comprises 15% of the total sperm protein, forms the fibrous bodies during spermatogenesis and becomes concentrated in the pseudopod during spermiogenesis (Ward and Klass, 1982). Similar sperm protein studies may reveal the composition of the fibrous bodies of *P. penetrans* and their role in sperm motility. Ward et al. (1982) demonstrated that *C. elegans* spermatozoa have a novel mechanism of motility called propulsion by bulk membrane flow. Future studies on *P. penetrans* and other plant-parasitic species may demonstrate similar mechanisms of motility and could provide insights into the composition and role of the fibrous bodies that represent the MSP found in a wide range of nematodes.

Many of the concepts of spermatogenesis and interactions of sperm motility studied in *C. elegans* and animal-parasitic species as reviewed by Scott (1996) should be applicable to plant-parasitic species. The uniqueness of nematode motility and sperm protein may be a target for the disruption of fertilization and possible control strategies for plant-parasitic nematodes.